SEED DISPERSAL ECOLOGY OF SQUAW-APPLE (ROSACEAE: PERAPHYLLUM RAMOSISSIMUM)

FINAL REPORT FOR RESEARCH AGREEMENT
#INT-94971-RJVA
"Seed Dispersal Ecology of Squawapple
(Rosaceae: Peraphyllum ramosissimum)"
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SEED DISPERSAL ECOLOGY OF SQUAWAPPLE

(ROSACEAE: *Peraphyllum ramosissimum*)

Final Report

by

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This research was supported in part by funds provided by the Intermountain Research Station, Forest Service, U.S. Department of Agriculture.

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INTRODUCTION

Squawapple (ROSACEAE: *Peraphyllum ramosissimum*) is a locally abundant, fleshy-fruited plant found on dry slopes in the Great Basin. Published data on its germination requirements is limited (Schopmeyer 1974), and ecological information is virtually nonexistent. This report contains results of a 1994 cooperative study designed to gather preliminary descriptive data on the phenology, reproductive success, and dispersal of squawapple. Incidental observations made in the years 1992–1995 are also included. Throughout this manuscript the pronoun *I* refers to the first author (J. Auger).

OBJECTIVES

We list below the objectives as outlined in the original proposal. Data were collected on all items with varying success. Quantitative data were obtained for items I B, I C, and II A 1. Good qualitative or anecdotal data were collected for items I A, II A 2, II B 1, and II B 2. Additionally, fruits were collected and frozen in anticipation of laboratory nutritional analysis (Objective III). Those are currently stored at the USDA-FS Shrub Sciences Lab, Provo, UT.

I. Fruit production will be characterized in terms of phenology, reproductive success, and reproductive output. Individuals in two populations will be sampled.
   - A. Fruit and seed phenology will be monitored, with an emphasis on ripening of seed in relation to changing appearance of fruit.
   - B. Reproductive success will be determined using flower to fruit ratios and ovule to seed ratios. Variation among fruits will be determined for the latter.
   - C. Reproductive output (i.e. fruit crop size in numbers and biomass) will be estimated per unit plant size and per unit area.

II. Aspects of primary and secondary fruit/seed dispersal will be characterized. Secondary dispersal will be addressed in the framework of rodent interactions with bear scats.

A. Primary dispersal.

1. The initiation, rate, and termination of fruit removal will be recorded.
2. Fruit/seed dispersers and predators will be identified.

B. Secondary dispersal.

1. The initiation, rate, and termination of seed removal from bear scats by seed predators will be recorded.
2. Seed predators/dispersers will be identified.

III. The nutritional content of squawapple fruits and seeds will be determined at varying stages of ripeness and also after digestion by a black bear.

METHODS

Sustained field work began on 5 July and ended on 12 August 1994 on the East Tavaputs Plateau of east-central Utah. Five major stands of squawapple were located and characterized (Appendix 1). Site names are associated with landscape features on USGS topographic maps: Hay Canyon, McCook Ridge, Mexico Point, Monument Ridge, and Willow Canyon (Fig. 1). Specific map coordinates are available from Hal L. Black. For some analyses the Monument Ridge stand was divided into two components: sagebrush (*Artemesia tridentata* and *A. nova*) dominated and mountain mahogany (*Cercocarpus montanus*) dominated.

PHENOLOGY

Throughout the field season I made frequent notes on the color and seed development in squawapple from various locations. I also caged one plant at the top of South Canyon with hardware cloth so that the persistence of fruit barring dispersal could be determined.

PHYSICAL CHARACTERISTICS OF RIPE FRUITS

While processing various squawapple collections, we measured fresh and dry weights of both fruits and seeds as well as diameters of fresh fruits. We took weights

only for fruits collected after 28 July 1994 and diameters for fruits collected after 19 July 1994.

REPRODUCTIVE SUCCESS

Flower to fruit ratio, locule to fruit ratio, ovule to seed ratio, and pollination rate were determined using a bagging method. At Willow Canyon two branches on each of 50 representative flowering plants were bagged with white netting following pollination. At Mexico Point 46 plants were bagged using the same methods. Plants were stratified into three flowering intensity categories and effort was made to generally equalize the number of individuals in each category (Table 1). Bagging was done on 11-12 June 1994.

Table 1. Number of bags per flowering intensity at two sites, 1994.

Flowering Intensity	Willow Canyon	Mexico Point
High	16	12
Medium	17	17
Low	17	17

The original protocol called for one bagged branch on each plant to be cut before seed ripening and the other to be cut at ripening; however, on 11 July, elk and/or cows began destroying bags by pulling them off the branches. Since I was able to obtain data on seed fill and abortion even at that early date, I cut and processed bagged branches from both populations as quickly as possible. Most were processed by 20 July, but I continued to find bag remnants throughout the field season. For each branch I counted both set and aborted fruit. The sum of those two values equals the number of flowers originally on the branch. I then cut each full fruit in half and counted locules, filled seeds, and aborted seeds. From these values I calculated number of ovules (two per locule), total set seeds (filled seeds plus aborted seeds), and number

of unpollinated ovules (ovules minus total set seeds) for each fruit. I also recorded frequency of caterpillar damage.

Reproductive Output

We had planned to estimate potential reproductive output for several squawapple stands using three pieces of information: density, size structure, and relationship between size and fruiting intensity. Time constraints and rapid fruit removal in 1994 prevented us from collecting the last piece for each stand, but ongoing analysis of the sizes of bagged plants may prove useful.

Density. The wandering quarter method described by Bonham (1989) was used to determine plant density. This method requires no assumptions of random distribution, and, if clumping occurs, can determine average within-clump and between-clump distances. Six sites were sampled: Hay Canyon, McCook Ridge, Mexico Point, Monument Ridge—sagebrush, Monument Ridge—mahogany, and Willow Canyon.

Size Structure and Associated Species. All plants on density transects as well as bagged plants were scored for size structure using a categorical system in three dimensions: height, crown, and fullness. Category boundaries are described in Table 2. . Any plant under 3 ft in either the height or crown dimensions was measured with a tape. Other woody plants growing in the same clumps as squawapple individuals were recorded.

Table 2. Description of height (h), crown (c), and fullness classes. Boundaries are given in feet.

Height		Crown		Fullness	
Class	Bounds (ft)	Class	Bounds (ft)	Class	Description
A	$h \leq 3$	i	$c \leq 3$	1	Branches willowy, straggly
B	$3 < h \leq 4.5$	ii	$3 < c \leq 5$	2	Branches compact, full
C	$4.5 < h \leq 6$	iii	$5 < c \leq 6.5$		
D	$h > 6$	iv	$6.5 < c \leq 7.5$		
		v	$7.5 < c \leq 8$		
		vi	$c > 8$		

Fruit Removal

At both the Monument Ridge Junction and McCook Ridge populations, I flagged one branch on each of 50 plants such that 15–30 fruits were above the marker. Fruits remaining were counted at 2–3 day intervals between 9 July and 30 July 1994, for a total of eight visits to Monument Ridge and nine to McCook Ridge.

Identification Of Dispersers And Seed Predators

I spent significant time making direct daytime observations in the squawapple patches (1) to look for bear sign and (2) to watch squirrels, chipmunks, and birds handling fruits and dispersing seeds. I also used three TRAILMASTER systems with cameras to photograph nocturnal visitors to seed-rich scats obtained by feeding squawapple to a captured bear. I set two systems in squawapple-dominated habitat (5 nights total) and one in a Douglas fir (*Pseudotsuga menziesii*) stand (4 nights).

RESULTS

Phenology

Two observations were made in June 1994. On 3 June squawapples all over the study area were in full flower and by 11 June some aborted flowers were abcissing. In the years 1992–1995, squawapples always flowered shortly after serviceberry (*Amelanchier alnifolia*), at the same time as snowberry (*Symphoricarpos oreophilus*), and before chokecherry (*Prunus viginiana*). Gorchov (1987) found that such relative phenologies are consistent within location over long periods.

Despite not flowering first, squawapple was always first to present colorful, fleshy fruits. On 8 July 1994 fruits were already yellow-red and fleshy, but seeds were just beginning to fill with bright white endosperm, and the seed coats were light-green and soft. Of note is that there seems to be a squawapple morph which produces only yellow fruits. Several such individuals were observed at McCook Ridge.

On 19 July seed coats were generally still green and soft, but by 21 July some had toughened and turned brown on the tips of the seeds. Fruits were considered fully ripe when seed coats turned leathery brown and flesh became soft and yellow-orange. This condition was first observed on 25 July at Monument Ridge and on 1 August on McCook Ridge. This criterion of ripeness may be faulty however, because "unripe" greenish-yellow seeds (collected 21 July 1994) are highly germinable in the laboratory even when they have been allowed to desiccate for two weeks prior to testing.

Fruits of squawapples reportedly drop from the parent plant (K.T. Harper, pers. comm.), but all fruit still remained on the caged plant on 12 August 1994. No observations were made after that date.

Physical Characteristics Of Ripe Fruits

Frequency distributions of fruit diameter for the McCook Ridge, Monument Ridge, and Willow Canyon populations are given in Figures 2, 3, and 4. One individual at the top of South Canyon was also sampled (Fig. 5). Table 3 contains the mean diameters and standard deviations for these four samples.

Table 3. Mean fruit diameters and standard deviations (SD) for four samples from the Book Cliffs, UT. Fruits from South Canyon were sampled from one individual only.

Location	Mean Diameter (mm)	n	SD
McCook Ridge	13.25	299	2.63
Monument Ridge	12.69	309	1.62
Willow Canyon	12.4	208	1.68
South Canyon	13.5	182	1.91

We estimated fresh fruit weight from two samples: one from Monument Ridge (864 fruits) and one from McCook Ridge (646 fruits). The values were 0.805 g/fruit and 0.796 g/fruit respectively. Eleven samples collected in 1992 yielded slightly higher mean weights ($\bar{x}$=1.199 g/fruit, SD=0.307), although a statistical comparison was not

made. During drying, fresh fruit weight dropped approximately 80% (2 samples), and seeds alone lost 35% of their fresh weight (3 samples).

To estimate dry seed weight we weighed six samples of 30 seeds each. Mean sample weight was 0.5666 g (n=6, SD=0.642). Converting this value to seeds per gram gives 52.9, which is in a more familiar form approximately 24,016 seeds per pound. This last figure corresponds closely with the estimate of Plummer et. al. (1968) which was 23,750 seeds per pound.

Reproductive Success

Overall, wildlife or livestock destroyed 25.5% of the mesh bags in the reproductive success sampling. Nevertheless, estimates of all parameters were obtained (Tables 4 and 5). Analysis using two-way ANOVA with population and flowering intensity as main effects is underway.

Squawapple reproductive success is not pollen-limited as evidenced by the low occurrence of unpollinated ova (Table 5). The pollinator diversity in and around squawapple stands observed by myself, S. Meyer, and B. Schultz (4 June 1994) was upward of 20 species. We saw various flies (Diptera) including bee flies (Bombyliidae), bees (Hymenoptera), and a hummingbird moth (*Hemaris thysbe*: Sphingidae).

Table 4. Mean fruit to flower ratios and locule to fruit ratios for two squawapple populations, 1994.

Population	Fruit/flower		Locules/fruit	
	$\bar{x}$ ± SD	n (bags)	$\bar{x}$ ± SD	n (fruits)
Mexico Pt.	0.393 ± 0.26	56	2.24 ± 0.45	376
Willow Cyn.	0.124 ± 0.13	87	2.86 ± 0.64	250

Damage to fruits was primarily caused by caterpillars of an unidentified micro-lepidopteran. At Mexico Point, 22% of the fruits in the bags were damaged, and at Willow Canyon 29% were damaged.

Table 5. Summary values (proportions) for pollination and seed set for fruits of two squawapple populations, 1994.

Population	Unpollinated		Aborted post pollination		Filled	
	$\bar{x} \pm$ SD	n	$\bar{x} \pm$ SD	n	$\bar{x} \pm$ SD	n
Mexico Pt.	0.007 ± 0.055	349	0.282 ± 0.280	349	0.710 ± 0.283	368
Willow Cyn.	0.020 ± 0.084	245	0.402 ± 0.280	245	0.577 ± 0.285	250

REPRODUCTIVE OUTPUT

Density. Six locations were sampled for squawapple density. The Hay Canyon, Monument Ridge—mahogany, and Willow Canyon locations all had randomly distributed individuals, and mean areas per plant were 95.5 ft^2, 144.3 ft^2, and 135.3 ft^2 respectively. McCook Ridge, Mexico Point, and Monument Ridge—sagebrush had clumped distributions of squawapple. Calculations of mean within-clump and between-clump distances are in progress for these three areas.

Size Class and Species Associations. Of the 596 squawapple individuals sampled by the wandering quarter method, 62% were smaller than 3 ft in both height and crown dimensions. Chi-square analysis indicates that proportion of these small plants depends on location ($\chi^2 = 54.96$, df=5, $p<0.01$). McCook Ridge and Monument Ridge, both dominated by mountain mahogany, had higher frequencies of larger plants, while the Hay Canyon and Monument Ridge areas, dominated by sagebrush, had the smallest size structure (Appendix 2). Plants under 3 ft in height and crown were not observed to flower prolifically in any year from 1992 to 1995. Moreover, only 11 of the 94 bagged plants were this small (Appendix 3), and 10 of them scored as low intensity flowerers in both 1994 and 1995.

Approximately 70% of squawapple individuals occurred in mixed-species clumps with the following woody associates: snowberry, mountain mahogany, sagebrush (*Artemesia tridentata* or *A. nova*), serviceberry, bitterbrush (*Purshia tridentata*), and

Gambel oak (*Quercus gambelii*). Occasionally squawapples occurred with pinyon pine (*Pinus edulis*) or juniper (*Juniperus*) species.

Fruit Removal

Because fruit numbers had decreased upon the first reading of marked branches, we assume that initiation date of fruit removal occurred prior to 14 July 1994. The discovery of two black bear scats containing squawapple on 9 July (Tom Patterson Ridge) confirms this assumption. Within 22 days (9–30 July) 91.5% of the marked fruit had been removed from the Monument Ridge population and 99.7% from the McCook Ridge population. Figure 6 shows the percentage of fruit remaining over time for both populations. Additionally, all fruit had been removed from the Mexico Point population by 17 July, except those damaged by lepidopterans.

Dispersers And Seed Predators

Throughout the study, the sight of least chipmunks (*Tamias minimus*) and golden-mantled ground squirrels (*Spermophilus lateralis*) climbing in squawapple bushes was most ubiquitous. Foraging chipmunks picked single fruits, immediately extracted the seeds, and discarded the flesh and skin onto the ground. I could not determine whether the seeds were ingested or cached. The large amount of debris underneath squawapple plants suggests that chipmunks predated a significant portion of the crop in 1994.

I often saw or heard blue grouse (*Dendragapus obscurus*) in mountain brush habitat, and on one occasion saw a hen pluck three fruits in succession from a low squawapple branch on McCook Ridge.

No black bears (*Ursus americanus*) were directly observed in squawapple patches, but on 22 July 1994 we observed bear tracks and freshly broken squawapple branches on McCook Ridge. Additional broken branches were observed on 30 July in the same area.

In both squawapple and Douglas fir habitats the TRAILMASTER systems photographed visits to seed-rich bear scats by deer mice (*Peromyscus maniculatus*) and least chipmunks. Seeds harvested from the scat piles were not quantified.

ACKNOWLEDGMENTS

We acknowledge and thank the volunteers who graciously helped with the preparations and field work for this project including Emily Dillon, Marlyn Dillon, Margaret Martin, Bettina Schultz, and Lori Tenney. We are most especially grateful to the Bureau of Land Management, Vernal District for providing facilities in the remote Book Cliffs which made life *comfortable* for extended periods.

LITERATURE CITED

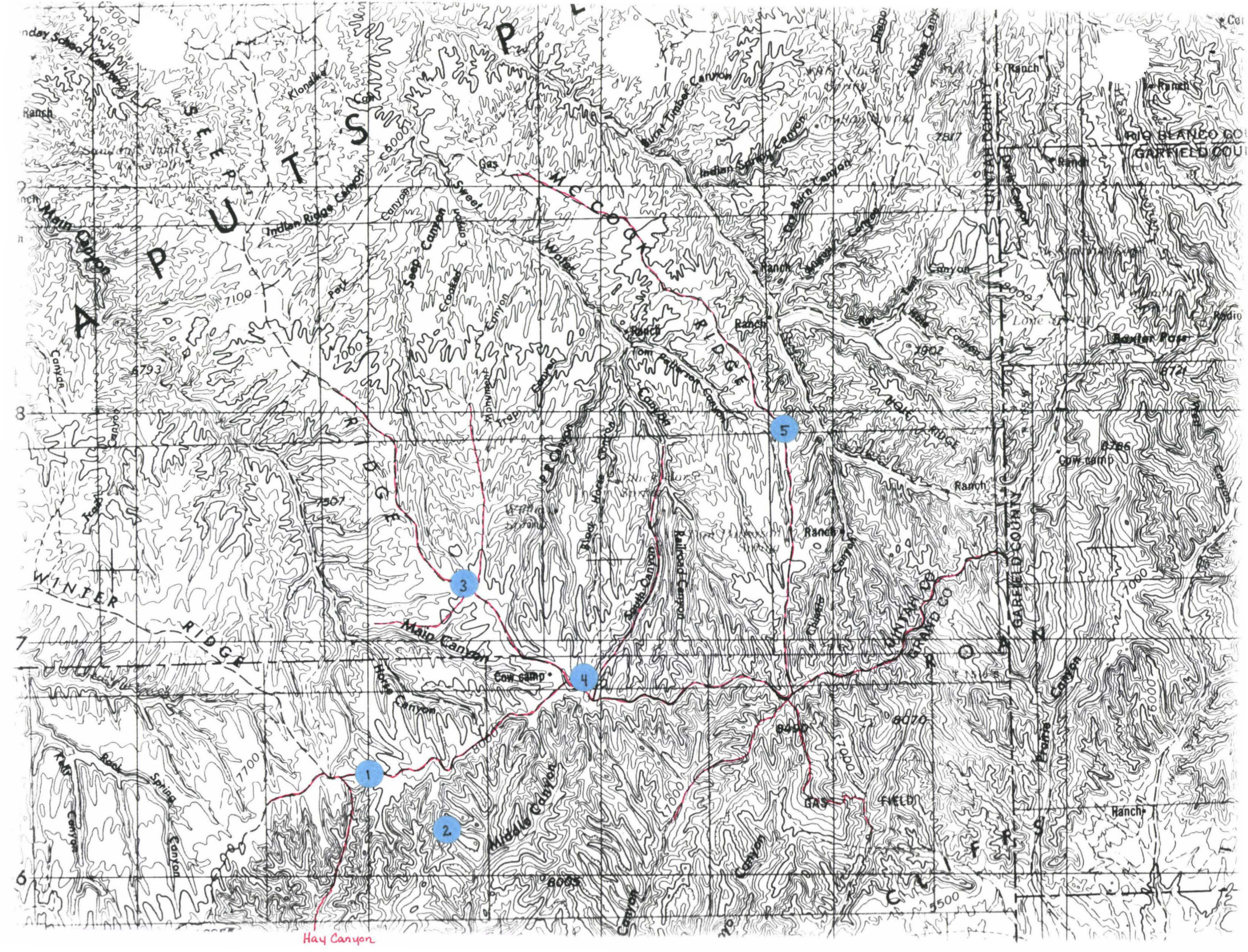
Bonham, C.D. 1989. *Measurements for terrestrial vegetation.* New York: John Wiley & Sons, 338 pp.

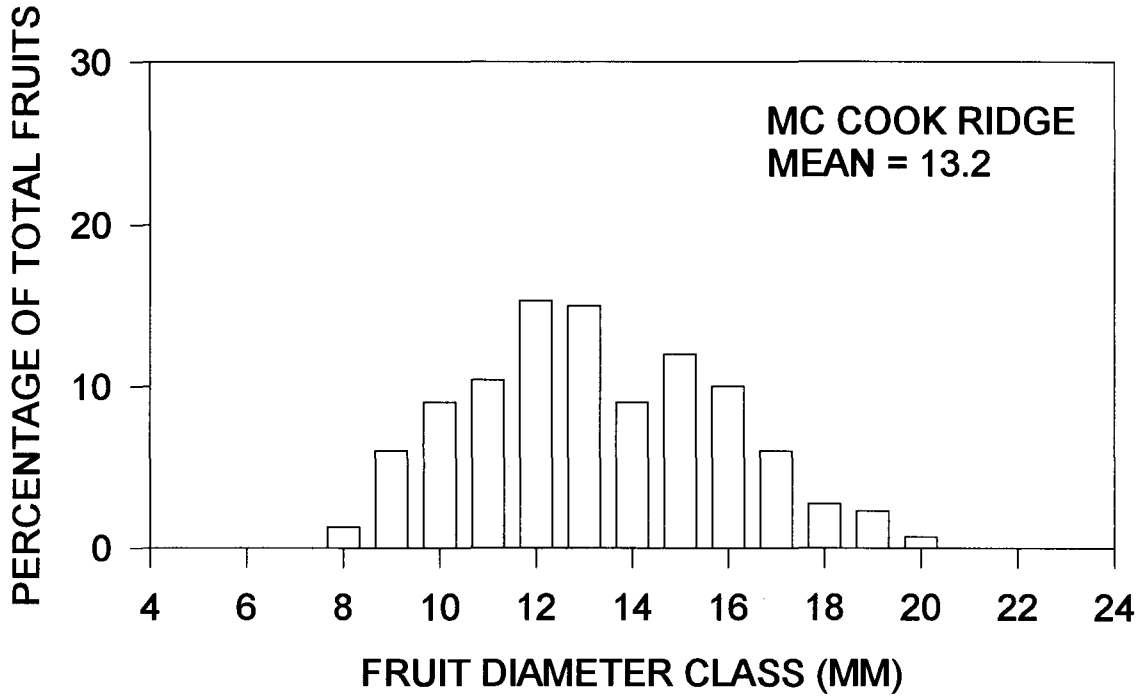
Gorchov, D.L. 1987. Sequence of fruit ripening in bird-dispersed plants: consistency among years. Ecology 68:223-5.

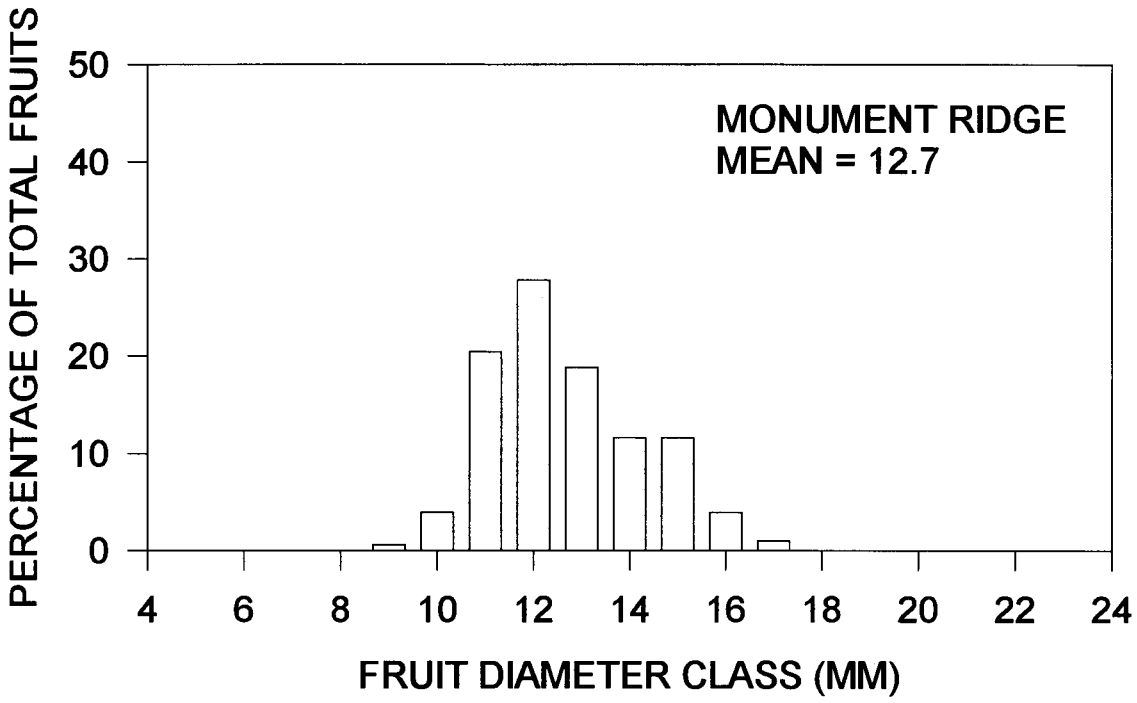
Plummer, A.P., D.R. Christensen, and S.B. Monson. 1968. *Restoring big-game range in Utah.* Utah Department of Natural Resources Division of Fish and Game Publication 68-3, 183 pp.

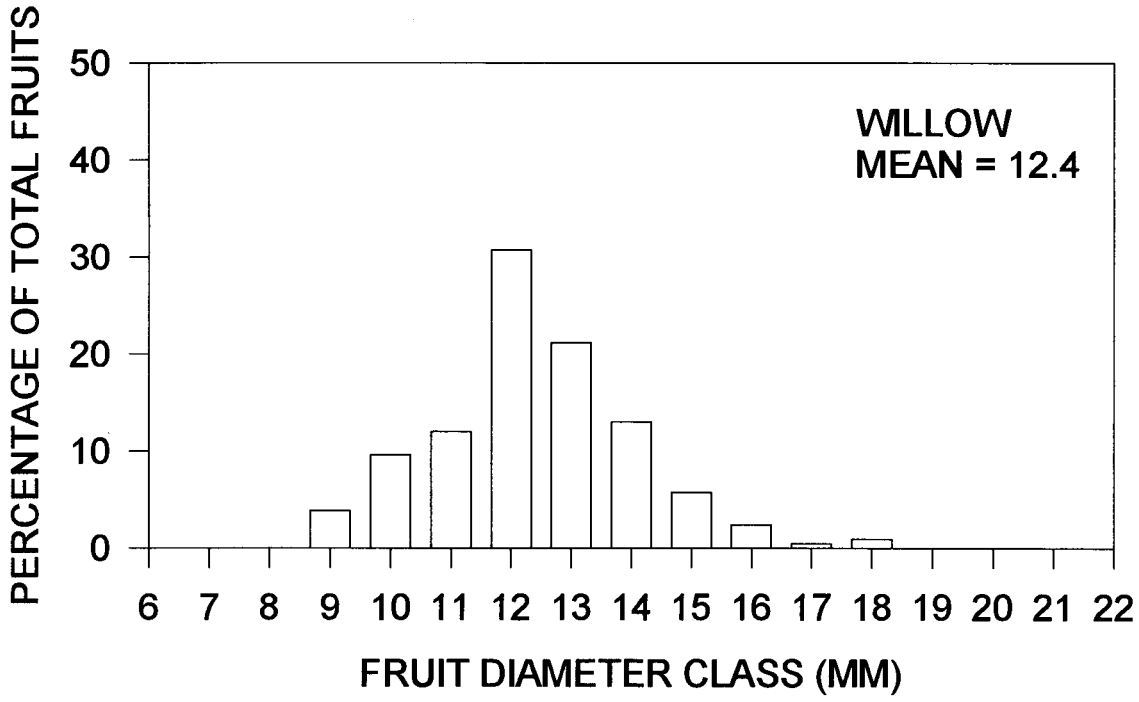
Schopmeyer, C.S. (Ed.) 1974. *Seeds of Woody Plants in the United States.* Forest Service, U.S. Department of Agriculture, Washington, D.C.

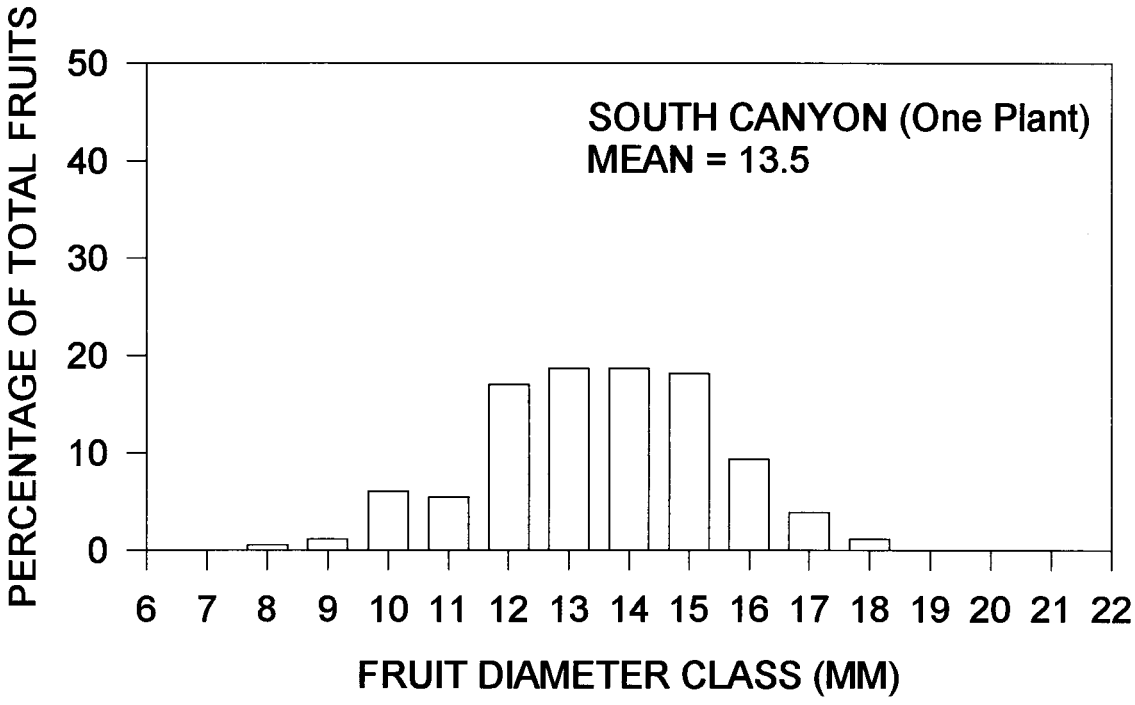
LIST OF FIGURES

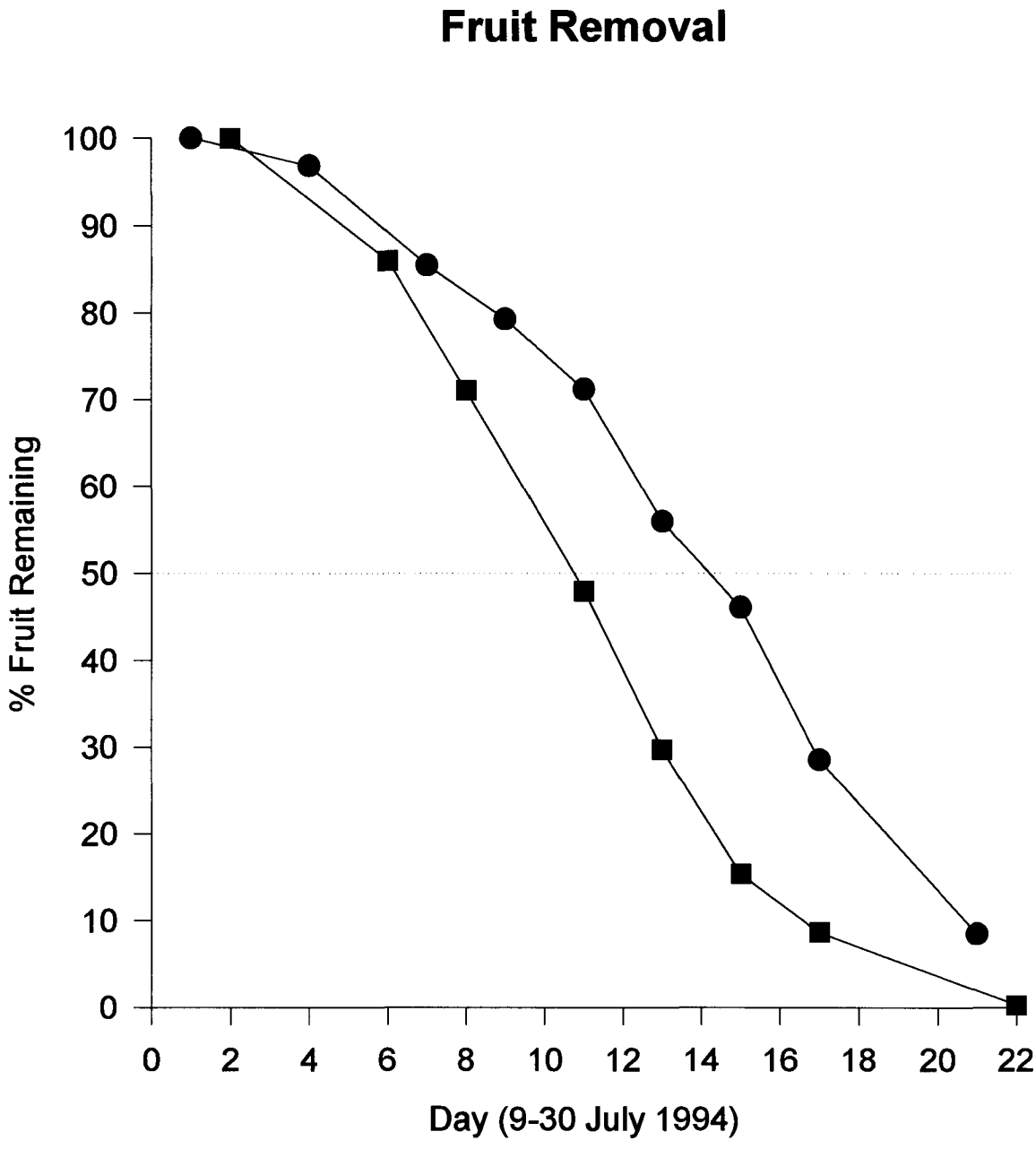

PARACHUTE
PUTTS
MCCOOK RIDGE
WINTER RIDGE
Main Canyon
Middle Canyon
Hay Canyon
Indian Ridge Canyon
Sweet Canyon
Seep Canyon
Horse Canyon
Cow Camp
Ranch
Baxter Pass
GARFIELD COUNTY
RIO BLANCO CO
GAS FIELD
1
2
3
4
5


PERCENTAGE OF TOTAL FRUITS
30
20
10
0
MC COOK RIDGE
MEAN = 13.2
4
6
8
10
12
14
16
18
20
22
24
FRUIT DIAMETER CLASS (MM)


PERCENTAGE OF TOTAL FRUITS
50
40
30
20
10
0
MONUMENT RIDGE
MEAN = 12.7
4
6
8
10
12
14
16
18
20
22
24
FRUIT DIAMETER CLASS (MM)


PERCENTAGE OF TOTAL FRUITS
50
40
30
20
10
0
WILLOW
MEAN = 12.4
6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22
FRUIT DIAMETER CLASS (MM)


PERCENTAGE OF TOTAL FRUITS
50
40
30
20
10
0
SOUTH CANYON (One Plant)
MEAN = 13.5
6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22
FRUIT DIAMETER CLASS (MM)


Fruit Removal
% Fruit Remaining
100
90
80
70
60
50
40
30
20
10
0
0
2
4
6
8
10
12
14
16
18
20
22
Day (9-30 July 1994)

APPENDIX 1

Squawapple stands were characterized by ranking the five dominant shrubby overstory species and simply listing significant understory species. Notes were made on soil structure, ground cover, use by livestock and wildlife, etc. On two plots it was necessary to describe each side of the road separately.

HAY CANYON

1. *Artemesia spp.*
2. SYOR
3. PERA
4. CEMO (scattered)
5. QUGA (scattered)

Understory: PUTR, *Castilleja*, *Aranaria congesta*, *Chrysothamnus*, *Lupinus*, patches of grass, deadwood and litter.

Few to no rocks on soil surface
30-40% open surface area
Plot heavily used by deer and especially elk. Cows present also.
Gently sloping down towards Hay Canyon (compass bearing: 260°)

MCCOOK RIDGE

1. CEMO
2. PERA
3. *Artemesia spp.*
4. QUGA (patchy)
5. SYOR

Understory: PUTR, *Opuntia*, *Chrysothamnus*, *Oryzopsis hymenoides*, various other grasses in patches.

Scattered conifer
Small brittle shale on the ground surface. Tracking difficult in this substrate.
PERA does not extend off the ridgetop.
35 to 50% open surface area
Plot heavily trampled by cows.

MEXICO POINT

1. AMAL
2. CEMO
3. SYOR, QUGA
4. PERA
5. *Artemesia spp.*

Understory: *Mahonia repens*, *Balsamorhiza Chrysothamnus*, *Aranaria congesta*, various grasses.

Scattered *Pseudotsuga menziezii*
Heavy cover, 20 to 30% bare ground
No rocks, soil fine and loose
No slope

MONUMENT RIDGE JUNCTION—EAST SIDE OF SEEP RIDGE ROAD

1. CEMO
2. PERA
3. AMAL
4. *Artemesia spp.*
5. SYOR

Understory: PUTR, *Petradoria*, *Penstomon caespitosus*, *Ipomopsis*, *Eriogonum umbelatum*, *Agropyron*, few other grasses.

Scattered conifers: PIED, PSME, *Juniperus*
Soil is loose - good for tracks
Foot-long rocks are moderately abundant. Small crumbly rocks present on soil surface, especially within 30 m of road.
Slight slope
Ground quite open, 60% open area

MONUMENT RIDGE JUNCTION—WEST SIDE OF SEEP RIDGE ROAD

1. *Artemesia spp.*
2. PERA
3. SYOR
4. AMAL (scattered)
5. CEMO (scattered)

Understory: *Eriogonum umbelatum*, *Petradoria*, *Penstomon caespitosus*, *Potentilla gracilis*, *Aster hisperus*, patchy grass.

45–50% open ground

WILLOW CANYON—NORTH SIDE OF DIVIDE ROAD

1. *Artemesia spp.*
2. PERA
3. SYOR
4. *Petradoria*
5. QUGA (scattered)

Understory: *Lupinus*, *Achillea*, *Penstomon caespitosus*, *Penstomon watsonii, Potentilla gracilis*, *Sitanion hystrix*, *Bromus carinatus*.

Hard-packed soil, few small rocks
East-facing gentle slope
15-20% open space
Penstomon spp. and grasses cover much of what is not game trail.
Sharp ecotone to CEMO and AMAL

WILLOW CANYON—SOUTH SIDE OF DIVIDE ROAD

1. *Artemesia spp.*
2. SYOR
3. PERA
4. QUGA (shrubby and low-growing)
5. CEMO

Understory: *Mahonia repens*, *Rosa woodsii*, *Lupinus*, *Achillea*, *Penstomon caespitosus*, *Petradoria*, *Bromus carinatus, Sitanion hystrix*, other grasses.

Soil contains small crumbly rock.
Game trails constitute the only open space.
15% open ground

APPENDIX 2

Size class frequencies for six areas sampled by the wandering quarter method (Bonham 1989). See Table 2 for legend.

SIZE CLASS	HAY	MCCOOK	MEXICO PT.	MONUMENT	MONUMENT--Sage	WILLOW
i A 1	50	37	23	28	41	36
i A 2	24	12	35	22	42	21
i B 1	3	1	5	3	-	2
i B 2	1	-	1	-	3	2
ii A 1	3	2	5	7	2	5
ii A 2	7	6	10	9	10	6
ii B 1	2	5	7	7	-	6
ii B 2	4	8	6	8	-	5
ii C 1	-	-	1	3	-	2
ii C 2	1	1	3	1	-	1
iii A 2	-	-	-	-	1	-
iii B 1	-	1	-	2	-	-
iii B 2	3	6	-	1	-	3
iii C 1	-	1	-	1	-	2
iii C 2	-	1	1	-	-	1
iii D 1	-	-	-	-	-	1
iv A 1	-	-	-	1	-	-
iv B 1	-	4	-	-	-	1
iv B 2	-	3	1	-	-	-
iv C 2	-	1	-	1	-	-
iv D 2	-	-	-	-	1	-
v A 2	-	-	-	1	-	-
v B 1	-	1	1	-	-	-
v B 2	-	2	-	-	-	-
v C 2	2	1	-	-	-	1
vi B 1	-	-	1	-	-	-
vi B 2	-	-	-	1	-	1
vi C 1	-	2	-	1	-	-
vi C 2	-	3	-	2	-	-
vi D 1	-	1	-	-	-	-
vi D 2	-	1	-	1	-	-

APPENDIX 3

Size class frequencies for bagged plants at the Willow Canyon and Mexico Point populations. See Table 2 for legend.

SIZE CLASS	WILLOW	MEXICO PT.
i A 1	5	3
i A 2	1	4
i B 1	-	1
i B 2	2	2
i C 1	4	1
i C 2	-	1
ii A 1	-	4
ii A 2	4	2
ii B 1	3	4
ii B 2	7	9
ii C 1	3	1
ii C 2	3	1
iii A 2	1	2
iii B 1	1	1
iii B 2	1	3
iii C 1	1	-
iii C 2	4	-
iv B 2	2	-
iv C 1	1	-
iv C 2	-	1
v B 2	2	1
vi B 2	-	1
vi C 2	-	1